

XXV.—On the Structure of the Mouth in Sucking Crustacea.
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20. The third type is that of *Hyperini*—a modification of the general type of Amphipoda, adapted for life in the light (large eyes) and powerful swimming about at the surface of the ocean. A parallel to this could not be expected amongst the heavy Isopoda; but we find one amongst Ulonata, where the Odonata occupy an exactly analogous position to that of Hyperini amongst Amphipoda. Their well-known teeming variety in general external appearance, from the thick-set form resembling a bean, to the most slender and elongate shapes, as well as in the development of the limbs for prehension, climbing, and attachment, is explained by the great variety of structure and mode of life of those (mostly gelatinous) marine animals to which they attach themselves. Their true relations to these are probably not yet fully elucidated; but the following account of the structure of their mouth will show that at any rate they appear extremely well equipped for peeling off and gulping down little bits of the bodies of such animals.

In illustration of this type we may examine the head of *Themisto libellula*, Mandl. Viewing it straight in front, we observe at once the analogy with the head of Odonata. The front, properly speaking, carrying the two pairs of antennæ, is deeply sunk between the eyes; and below it the clypeus is seen to protrude like a hood; the terminal portions of all the appendages of the mouth are, as it were, folded together so as to form a perpendicularly descending inverted cone; the stipites of the mandibles form a slightly trisinate frame on either side of the flat bilobate upper lip; whilst the mandibular palpi, when at rest, fit closely under the lateral margins of the clypeus, the slender middle joint of each ascending perpendicularly in the hollow of the front, and the small pointed terminal joint crossing its opposite neighbour below the upper antennæ. Below the upper lip the palpi and the apices of the stipites of the first pair of maxillæ are seen somewhat foreshortened, whilst the second pair of maxillæ are hidden behind the palpi of the first pair and the anterior ends of the lobes of the maxillipeds, which are turned upwards and forwards, constituting the downward-pointing apex of the cone formed by the oral limbs. This view already discloses that the lobes of the mandibles are entirely covered by the upper lip. If we next examine the head from the side, we observe moreover

that the mandibles in the whole of their extent are of unusual height, almost as high at their apex as at their base, and consequently, in this respect, very different from what is seen in the two preceding types. We observe besides that the mandibular springs of the lower lip are so short that they by no means, as in *Eleutherognathia* and *Trochalognatha*, almost reach as far back as the inner corners of the bases of the mandibles; finally, it is seen that the second pair of maxillæ are to that extent involved by the maxillipeds that only a small strip of their middle portion becomes visible without preparation. The proportion in which the different oral limbs take part in the composition of the cone described appears still more clearly if this is examined from below, facing the apex of the cone: the lower margin of the mandibles is seen uncovered, whilst the second pair of maxillæ are entirely hidden except the middle portion, the narrow maxillipeds covering the central part of the cone with their coalesced minor lobes. If we bend the maxillipeds back, it is easily perceived that their use is to cover the maxillæ and fill out the space left between them; the upper face of the stipes is carinate and fits in between the second pair of maxillæ; the inner lobes are coalesced and close the space between the grinding-teeth of the mandibles; the outer lobes fill out the space all the way forwards to the upper lip, covering the inner parts of the first pair of maxillæ. The maxillipeds have no palpi. The second pair of maxillæ are distended, cushion-like; and only the apices of their lobes carry spines and setæ. The first pair of maxillæ have large cardines, large stipites with dilated apices, but no inner lobes; the outer lobe of each maxilla carries on its apex five powerful spines arranged in two rows, and a considerable number of stiff setæ. The palpus consists of but one joint, broad, oval, arched, with truncate apex, which is furnished with smooth and ciliated spines; whilst the inner margin is slightly curved and serrate, with a small spine in each indentation of the saw, and a short thick thorn in the inner corner. If now, finally, all the appendages of the mouth are taken away except the mandibles (as we have done in examining the previous examples), the hypostoma appears, with the articular sockets of the two pairs of maxillæ, and also the whole of the lower lip. The short and broad form of the latter reminds us of *Caprella*, whilst the inner lobes are still more reduced than in *Anonyx*; but the mandibular springs are much thicker than in either of these two types, and of a peculiar curved shape. At the same time the anterior lobes, though in shape and thickness rather recalling the same parts in *Caprella*, differ from

those of both Eleutherognatha and Trochalognatha in this essential particular, that they do not touch each other with their apices, but leave a broad space between them, whilst in front they fit close against a transversal arched kind of bolster, thicker towards both extremities, and belonging to the upper lip, but separated by a deep and broad furrow from the bilobate leaf of the upper lip, which is visible outside on the head. From the centre of this transversal cushion, backwards to the hypostoma, a narrow serrate seam appears, which the observer in the first instance, without special examination, is inclined to interpret as being formed by the interior margins of the middle lobe of the lower lip touching one another in the median line; if, however, the lateral lobes of the lower lip are now cut away, it becomes evident that the middle lobes are entirely absent, and that the serrate seam in question is formed by the inner margins of the large flat grinding-teeth of the mandibles, which consequently occupy the whole space between the transversal cushion of the upper lip, the lateral lobes of the lower lip and the hypostoma, thus entirely closing up the palate from below. The latter does not appear until the mandibles are opened; and it is then seen that behind the transversal ridge of the upper lip there is on the palate a low semicircular eminence, and along the median line, just above the serrate inner margins of the grinding-teeth, a narrow depression forming a sort of canal, leading to the opening of the pharynx. Outside and behind the lateral lobes and mandibular springs of the lower lip, the long and very high stipites of the mandibles are seen, whilst their narrow, sharp, edgewise-set outer lobes fit into the transversal furrow above mentioned, between the foremost bilobate leaf of the upper lip and its transversal ridge or cushion. Examined from the fore end, after the removal of the anterior bilobate part of the upper lip, the lobes of the mandibles show the form of two short saws with curved blades—the arched edge, which is coated with enamel as hard as glass, being cut into a row of sharp saw-teeth, increasing gradually in size towards the lower corners of the inner lobes, where the last two teeth, particularly the lower one, are considerably enlarged and developed into a pair of exceedingly sharp, incurved, prehensile hooks. The lobe of the left side glides above the one of the right side. If the parts are turned round and examined from the back, we perceive that the right mandible is entirely without inner lobe, whilst the left mandible possesses one placed behind the upper half of the outer lobe, and of the same structure, excepting that the teeth of the saw are all of equal size and that there are no prehensile hooks; the outer

lobe of the right mandible fits into the cleft between the outer and inner lobes of the left; so that the cutting is done by three saw-blades—two from the left side and one from the right, which latter cuts in between the two former.

This remarkable combination obtains with small variations through the entire series of Hyperini, which otherwise presents such different forms. With reference to its principal character, the fitting of the mandibular lobes into a groove or hollow in the upper lip, the Amphipoda of this type may be called *Piezognatha*.

21. We have then the following formulas for the three types in the structure of the mouth in biting Amphipoda:—

ELEUTHEROGNATHA.

Mandibulæ trigonæ, condylo articulario antico carentes.
Labrum planiusculum, transversum, simplex.

TROCHALOGNATHA.

Mandibulæ productæ, condylo articulario instructæ antico,
acetabulo epipharyngis accommodato.
Labrum crassum, conicum, simplex.

PIEZOGNATHA.

Mandibulæ productæ, condylo articulario antico carentes, mala
exteriore fossæ transversæ labri accommodata.
Labrum planiusculum, transversum, duplex.

22. Amongst the series of forms exhibiting the eleuthero-gnath type, there are several which simulate more or less strikingly the build of other types. One of the most remarkable is *Stegocephalus*, reminding us in general appearance of the trochalognath *Anonyx*, whilst its enormously developed face and the armament of the mandibles approach more to the piezognath *Hyperia*.

The clypeus, labrum, palate, two pairs of maxillæ, and the maxillipeds, as well as the mandibular springs of the lower lip, correspond in all essential respects to the general features of the type. The upper lip is bilobate, the right-hand lobe larger than the left. But the mandibles are quite without grinding-teeth, the right mandible also without an inner lobe; and though the left mandible possesses the hard branch of the latter, which has a long finely serrate margin, it lacks the membranaceous digitiform appendages; the outer lobes of both mandibles have each a long, curved, finely serrated edge, almost as in Hyperini, but with the essential difference that all the saw-teeth are here equally large,

the lower ones not being developed into prehensile hooks. Furthermore the middle lobes of the lower lip are quite missing, and the foremost ones are so small, narrow, and thin as to be unable to fill the space between the mandibles, in consequence of which the palate here, as in *Anonyx*, is quite uncovered as soon as the maxillipeds and the two pairs of maxillæ are taken away.

23. But the extremest place inside the boundaries of Eleutherognatha is occupied by the læmodipodous *Cyamus*, so peculiar by its flattened shape, hooked legs, and general equipment for attaching itself to the skin of whales, which it gnaws to pieces and gulps down. The structure of its mouth has been hitherto known only from the schematic outline by Savigny. It will be seen from the following account what considerable alterations in the shape and relative position of the appendages of the mouth have been necessary, in order to enable the animal to press the mouth against the extensive firm surface which it has to penetrate and to which it must cling. The usual arrangement of the organs (like strata, or leaves of a book), by which the oral limbs generally in Amphipoda are collected into a thick package under the head, has here been abandoned, the most active instruments for gnawing (the mandibles and the first pair of maxillæ) having been proportionately expanded and flattened; whilst the lower parts, which support and enclose the former, viz. the second pair of maxillæ and the maxillipeds, are considerably reduced in development or pushed out to the sides. Above all, the lower lip has lost the part which it has to play in other Amphipoda, as in forming a kind of spring for the mandibles; so that it corresponds entirely to the conformation of the tongue in Isopoda. Finally, the equipment with spine and setæ has almost entirely been replaced by an equipment with organs of touch.

The anterior extremity of the head presents a small oval surface, surrounded, as far as the broad, shortly bilobate upper lip, by the palpi of the maxillipeds, forming a sort of raised margin when seen from above. These palpi are long and stout, without claw, and consist of five joints, which only at their apices carry a few pointed setæ, the last but one being furnished at the apex with a larger number of thin tactile setæ; some tactile warts are observable on the apex of the last joint; and this latter also has a small comb of delicate spines on its inner margin. The broad, flat, almost quadrangular stipites of the maxillipeds are so short that they only cover the space behind the second pair of maxillæ; the lobes, moreover, are entirely absent, or only represented by the slightly expanded and rounded outer corners of the stipites, which

carry a row of tactile setæ. In consequence of these circumstances, both pairs of maxillæ are uncovered unless the palpi of the maxillipeds happen to be in an inward-bent position, in which case they can cover the outer portions of the first pair of maxillæ and also the dorsal margin of the mandibles, which appear behind their outer lobes. The maxillæ of both pairs being thus uncovered, it devolves on them to cover the hypostoma, which is otherwise mostly done by the lobes of the maxillipeds; and accordingly the second pair of maxillæ assume an aspect which reminds us in a high degree of the maxillipeds in Isopoda. Their stipites coalesce entirely, forming an obovate flatly arched piece, which covers the hindmost part of the hypostoma in the middle, from the cleft between the stipites of the maxillipeds forward to the bases of the lobes of the first pair of maxillæ. The inner lobes of the second pair are placed close together in the median line of the head; and their rounded apices carry each one stout tactile seta: the outer lobes are small, triangular, and inserted on a level with the narrow bases of the inner lobes; and their rounded apices carry two rows of more slender tactile setæ—one row on the upper surface, the other on the edge. The apices of all the lobes of the second pair of maxillæ reach forward as far as the middle of the inner margin of the outer lobes of the first pair of maxillæ, and a little beyond the base of the lower lip; the second pair of maxillæ therefore cover altogether only a small space in the middle of the hypostoma, but leave the maxillæ of the first pair entirely uncovered. The covering of the hypostoma on the sides towards the pleural margin of the head, devolves consequently on the first pair of maxillæ, which to this end are equipped with cardines of enormous size, much larger than are necessary for the purpose of the articulation of the limb, being expanded outwards from the sockets into a pair of obovate flatly convex plates, placed aslant, each of which is divided a little behind the middle into two halves by a curved transverse groove on the lower face, corresponding to a ridge in the interior, on which the flexor muscles are attached; the stipites of this first pair of maxillæ are, for the same reason, of unusual width. There is no inner lobe; but the outer lobe is broad, along the inner margin armed with small hooked setæ, whilst the obliquely truncate apex carries seven stout, deeply inserted, conic, slightly incurved spines, which have a prominent serrate ridge on their lower surface, a little inside the inner margin; the spines form two rows, the upper row consisting of four, the lower of three spines. The very short and slender palpus consists of only one conic

joint, which scarcely reaches beyond the first third of the outer lobe, and on its truncate apex carries a considerable bundle of thin tactile setæ. The lower lip reaches to the base of the terminal spines of the first pair of maxillæ and the inner corners of the outer lobes of the mandibles; as already indicated, it resembles entirely the tongue in Isopoda, narrow at the base, a little wider at the apex, and there divided into four lobes with small and delicate spines on their apices, the two lateral lobes being longer, obtusely pointed, diverging, and slightly incurved, whilst the two middle lobes are small, pointedly rounded, leaving a narrow split in the middle line of the mouth. The mandibles, too, resemble strikingly the same organs in Isopoda: they are remarkably small, reaching backwards only as far as the middle of the stipes of the first pair of maxillæ, but are nevertheless strongly built in proportion. The upper surface of the stipes is in the middle strewn with exceedingly small warts. There is no palpus; but both lobes are present, though those on the right mandible are not a little different in structure from those on the left. Examining the right mandible from above, the outer lobe is seen to end in five short thick teeth forming a transversal row, of which the innermost is somewhat outward-bent and covered by the inner lobe, whilst the outermost tooth is placed a little above its next neighbour, and this again a little over the nearest of the two middle teeth. Accordingly, when we examine the same mandible from below, the outer lobe is seen to cover the inner lobe to some little extent; and on account of the arrangement of the teeth just described, there appear in this position to be only four on the outer lobe instead of five. The outer lobe of the left mandible, on the contrary, has six teeth on its apex, placed in two rows, diverging towards the inner side, shorter and much less incurved than those on the two lobes of the mandible of the opposite side, between which they fit in. The differences between the inner lobes of the two mandibles are still more considerable. On the right mandible the anterior portion of the inner lobe is of about the same structure as the outer lobe: it terminates in a thick incurved tooth; and its anterior margin carries three thick teeth, which are placed on a lower level than the terminal tooth, but otherwise resemble it in shape and size; behind this anterior portion, with its hard enamel and armature of teeth, follows a thin closely ciliated membranaceous portion, of which the apex is cleft into six thin digitiform lobes. On the left mandible, on the contrary, the anterior part of the inner lobe lacks both enamel and teeth, and is represented by a short protuberance, with small warts on its sides and with a small slightly undulated

apical face, which, viewed from above, looks as if it had three obtuse teeth; the membranaceous portion is larger than on the right mandible, but has only three digitiform lobes.

24. Finally the cleuthernognath type appears in a remarkable modification in *Laphystius*, Kr., the only genus of sucking Amphipoda which I have hitherto been enabled to submit to a close examination. It occurs behind the pectoral fins of sturgeons, sharks, and the large cod; and Kröyer describes it as "unicum, quod adhuc innotuit, inter Gammarina animal parasiticum" (Naturh. Tidsskr. iv. p. 157). From his point of view and by his method of investigation, we could not expect that he should have understood that its mouth really was constructed for suction; at the same time his excellent diagnosis lays proper stress both on the broad figure of the animal, and on its hooked claws well adapted for holding on with, its "caput rostratum," the clumsy antennæ with their short stipites, the narrow mandibles, and the fact that the palpus of the first pair of maxillæ only consists of one joint, that of the maxillipeds of two.

The head is very small, with very prominent round eyes, consisting of large, strongly convex, closely collected ocelli. Viewed from the sides it presents but few features different from those of the ordinary *Gammarus*-type; nor do they at once strike the observer. The elongate-triangular dorsal face of the mandibles, the mandibular springs of the lower lip, the position and arrangement of the two pairs of maxillæ and the maxillipeds, as well as of the clypeus and labrum covering the parts of the mouth in front, present at first sight nothing to make us suspect any very remarkable peculiarities. On closer examination, however, three points will attract attention as indicating something out of the common, viz.:—first, the unusual height of the forehead and the pleural margin of the head; secondly, the circumstance that the terminal two fifths of the length of the mandibles are quite hidden by the upper lip; and, thirdly, that the lobes of the maxillipeds join the upper lip with their apices and lateral margins so closely that the lip and the lobes together form a beak-like eminence, which stands out separately from its surroundings on account of the great convexity of the lobes of the maxillipeds and the smallness of their palpi, which are so much reduced in size that they do not even reach quite to the lateral margins of the upper lip.

It is only when we examine the head from the front that its peculiar rostrate configuration becomes clearly appreciable. The outline of the face, strictly speaking, is a rhomb, enclosed by almost straight lines; the height from the apex of

the small frontal horn to the apex of the lobes of the maxillipeds exceeds by about one fifth the width across the round prominent eyes. The clypeus is of about equal height and width, rather convex, rounded above, the sides being also curved outwards. The upper lip is half as long again as the clypeus, highly convex, with pointed apex, the sides being outward-curved near the base, slightly emarginate towards the apex; on either side of the upper lip a small portion of the stipes of the mandibles appears, whilst their very long and stout palpi lie close to the forehead, ascending on either side of the clypeus; their terminal joint is very long, one fifth longer than the middle joint, conical, slightly incurved, pointed, furnished with short and long setæ on the apex and along the inner side. The terminal joints of the two palpi cross each other in the margin between the two pairs of antennæ. The downward-pointing angle of the facial rhomb is formed by the outer lobes of the maxillipeds lying close to the upper lip, and rolled together one with another.

If, in the next place, we proceed to dissect the head, beginning from behind, we meet, of course, first the maxillipeds. Their cardines and stipites are prolonged, each pair by itself entirely coalescing, and all together forming a club-shaped convex peduncle for the terminal parts (lobes and palpi), with rounded base, emarginate sides, and rounded sinuate anterior margin. The outer lobes are considerably shorter than the cardines and stipites together, and lie close together, the inner margin of the left involving that of the right; they are convex, cup-shaped, with broadly rounded apex when seen together, but each by itself pointedly rounded at the extremity; the outer margin has close fine hair, whilst the anterior part of the inner margin is finely serrulated with a few shorter setæ at the apex and on the under surface. The palpi are very thin, sparsely furnished with setæ only at their extremity; they do not reach forward so far as the apex of the outer lobes, and consist of only two joints of about equal length, of which the terminal one is straight, conical. The inner lobes of the maxillipeds are very small, not half the length of the outer lobes, conical, with a couple of small setæ on the rounded apex; and they are hidden under the inner margin of the outer lobe in such a manner that they do not appear before the maxilliped is turned entirely round so as to show its upper surface. The second pair of maxillæ has the form usual in Gammarini, with two flat lobes, the outer lobe being linear, slightly outward-bent, carrying on its broadly rounded apex seven thin, pointed, slightly incurved spines, ranged in an upper and a lower row; the inner lobe is falciform, shorter than the outer lobe, and

carries seven spines, scattered from the point downwards along the inner margin, of the same description as those of the outer lobe, only a little stouter and shorter. The first pair of maxillæ is especially distinguished by its rudimentary palpus, which does not reach forward beyond one fourth of the outer margin of the outer lobe, and consists of only one conical joint, with two setæ on its truncate apex. The outer lobe is narrow, falciform, and carries from the point downwards, along the anterior third of the inner margin, eight long, thin, incurved, very pointed spines arranged in an upper and a lower row, and behind them, further back, four other short and stiff scattered setæ; the inner lobe of the first pair of maxillæ is very small, with three delicate spines at the apex, and reaches scarcely so far forward as the apex of the palpus.

If now we finally remove all the just mentioned appendages of the mouth, the most remarkable feature of its construction appears, viz. that the middle and lateral lobes of the lower lip are not distinguishable from one another, so that there is really only one lobe on either side, the right-hand one involving to some extent the one on the left side; in front, the two short, rounded, linguiform apices diverge a little, so that the extreme ends of the mandibles appear between them; the mandibular springs of the lower lip are narrow, and their ends, which are a little outward-bent, reach not quite to the base of the mandibles. It is clear from this construction that it is here the lower lip which, by its peculiar modification of the shape usual in *Gammarini*, has been adapted to form the innermost enclosure of the oral tube, whilst the outer lobes of the maxillipeds supply its outer enclosure. If now, finally, the mandibles are laid bare by the removal of the lower lip, their configuration shows not a little similarity to that described in *Æga*. The stipes, on which the palpus is inserted closely in front of its outer corner, is narrow, thinner in front, gradually passing into the very narrow and long outer lobe, whose flat rounded apex carries six minute saw-teeth; the inner lobe is very small, membranaceous, narrow, terminating in three slender and pointed digitiform lobes.

A comparison between this combination and the forms of sucking-mouth described above in *Isopoda* discloses the remarkable difference, that the back wall of the rostrum in *Laphystius* is formed by the lower lip to the exclusion of the two pairs of maxillæ, of which, therefore, the first has been subject to very little modification, the second to none at all, as compared with the usual construction for biting-purposes; whilst in sucking *Isopoda* the back wall of the sucking-tube is formed by the second pair of maxillæ, whereby the first

pair of maxillæ are enclosed within the tube and have assumed a shape adapted to action inside it. Whilst, therefore, the rostrum in Isopoda contains mandibles and the first pair of maxillæ, *Laphystius* occupies the important stage in the development of the sucking-mouth in Crustacea where the rostrum only contains mandibles. The oral formula for *Laphystius* will consequently be the following.

Laphystius.

Os haustellum.

Haustellum aduersum clypeo labroque, auersum labio malisque exterioribus pedum maxillarium confectum, malas mandibulares serratorias involuens.

Clypeus rotundate quadratus, fornicatus, pendulus.

Labrum maximum, productum, conicum, acuminatum, fornicatum, pendulum.

Mandibula stipite producto, angusto, acuminato, depresso, mobili, basi palpigero, malis binis. *Mala exterior* sub labrum oblique inflexa, fixa, in orificium haustelli deorsum eminens, linearis, margine terminali arcuato, serrato. *Mala interior* basi malæ exterioris inserta, membranacea, mobilis, minuta, linearis, apice trifida. *Palpus* clypeum amplectens, triarticulatus, pervalidus, articulo terminali inter antennas recepto, producto, conico, acuminato, introrsum breviter setigero.

Maxilla priores laminatæ, malis binis, palpigeræ. *Mala exterior* falcata, apice spinis longioribus, validioribus, incurvis, in series binas redactis armata. *Mala interior* brevisima, conica, apice parce spinigera. *Palpus* perexiguus, conicus, singulo constans articulo, conico, apice truncato, breviter biseto.

Maxilla posteriores laminatæ, malis binis. *Mala exterior* linearis, apice spinigera. *Mala interior* falcata, margine inferiore parce spinifero.

Pedes maxillares cardinibus stipitibusque concretis, productis, fornicatis, malis binis, palpigeri. *Malæ exteriores* amplæ, sinistra dextram obvolvete, fornicatæ, apice late rotundatæ, labro contigua. *Malæ interiores* perminutæ, conicæ, malis exterioribus contactæ. *Palpi* minuti, conici, biarticulati, malis exterioribus manifesto breviores.

Labium amplum. *Processus* mandibulares angusti, acuminati, retro directi. *Lobi* intermedi in lobos laterales confusi, amplissimi, fornicati, dextro sinistram obvolvete, apice lingulati, mandibulas præter apicem malæ exterioris contingentes.